Macro-Epifauna of the Lower Bay of Fundy - Observations from a Submersible and Analysis of Faunal Adjacencies

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MACRO-EPIFAUNA OF THE LOWER BAY OF FUNDY - OBSERVATIONS FROM A SUBMERSIBLE AND ANALYSIS OF FAUNAL ADJACENCIES

by

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ABSTRACT

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Macro-epifauna on the Digby scallop grounds in the Lower Bay of Fundy were observed during six submersible dives in water depths ranging from 75 to 107 m. Observed adjacencies of fauna along transects were analyzed by using a run-like statistic.

Fifty-two taxa were observed. Sea anemones were the most frequent, followed by scallops, hermit crabs, sponges, whelks, and urochordates. The largest number of taxa was encountered at the deepest station. Epifaunal community zonation by depth and sediment type was evident.

Only 10% of the observed faunal adjacencies were non random. Most of these adjacencies involved a predator and an animal from a different trophic level. Some of the adjacencies may have reflected common requirements for a specific physical environment, provision of shelter, or commensalism.

RÉSUMÉ

Caddy, J.F. and J.A. Carter. 1984. Macro-epifauna of the Lower Bay of Fundy - observations from a submersible and analysis of faunal adjacencies. Can. Tech. Rep. Fish. Aquat. Sci. 1254: v + 35 p.

On a observé la macro-épifaune des fonds à pétoncles de Digby dans le bas de la baie de Fundy à l'occasion de 6 plongées en submersible à des profondeurs variant de 75 à 107 m. On a fait l'analyse statistique des données recueillies sur la faune adjacente dans les transects.

On a vu 52 taxons. Les anémones de mer étaient les plus répandues; viennent ensuite les pétoncles, bernard-l'hermite, éponges, buccins et urocordés.

C'est à la plus grande profondeur qu'on a observé le plus grand nombre de taxons. Il est évident que la répartition de la communauté épifaunique était fonction de la nature des sédiments et de la profondeur.

Dans 10% des cas seulement, la présence d'animaux à proximité n'était pas accidentelle. La plupart du temps, il s'agissait d'un prédateur et d'un animal d'un niveau trophique différent. Dans certains cas, il se peut qu'ils aient eu des besoins semblables quant aux caractéristiques physiques du milieu ou au type d'abri recherché ou encore, il pouvait s'agir de commensalis.

INTRODUCTION

Benthic fauna in the Lower Bay of Fundy have been sampled by a variety of methods including grabs and dredges (Caddy, 1970a; Wagner, 1979; Peer *et al.*, 1980). Grabs do not collect epifauna efficiently. Dredges and bottom trawls are an improvement; however, catch efficiency of trawls can be less than 10% of the real density of epifauna (Dyer *et al.*, 1982). Caddy (1970a) reported on the associated fauna collected in scallop dredge hauls in the Lower Bay of Fundy and noted the constituent species of benthic assemblages. However, he recognized that pooling of fauna in a dredge towed for up to 1.5 km could obscure real associations between epifaunal taxa. Bottom photography can record associations between epifauna, but high turbidity near the bottom in the Bay of Fundy is a problem. Observation from a submersible is one effective way to record discrete faunal assemblages on hard bottom in deep water. Submersibles have been used to estimate the population density of scallops (*Placopecten magellanicus*) in the Gulf of St. Lawrence (Caddy, 1970b) and to observe herring spawning grounds on Georges Bank (Caddy and Iles, 1973).

This report summarizes data on macro-epifauna on the Digby scallop grounds collected during observations from a submersible in September 1969. The study was the first attempt of its kind to observe deepwater fauna in the Lower Bay of Fundy other than by remote means such as dredging and photography. Two objectives of this study were to record the nature of epifaunal communities on the Digby scallop grounds and to test the applicability of a run-like statistic (Knight, 1974) to the recorded data.

MATERIALS AND METHODS

FIELD PROGRAMME

During the period September 10-13, 1969 six dives were conducted on the scallop grounds off Digby, N.S. (Fig. 1) in depths of water ranging from 74.7 to 106.7 metres. A seventh dive (Dive 3) was conducted in shallower water and is not discussed in this report. The Perry Submarine *Shelf Diver*, manned by four personnel, operated from the mothership CCGS *C.D. Howe*.

During each dive a continuous photographic record of scallop populations was supplemented by direct counts of scallops registered on an event recorder. Data from these observations were reported elsewhere (Caddy, 1976). Observations of fauna were registered on a tape recorder. An odometer wheel towed behind the submersible continuously recorded the distance travelled over the bottom. More detailed logistics of the diving procedure, navigation, scientific instrumentation, and viewport calibration were noted by Caddy (1976).

Observations of fauna were made through a forward viewport and recorded once the submersible had achieved a relatively stable course after descent. The heading, duration of observations, distance travelled over the bottom, and the range of depth of the submersible during the faunal observations of each dive are noted in Table 1. The observer limited his observations to the view plane directly in front of the submersible and entered taxonomic names as fauna were encountered. Once the submersible had begun a stable course along the bottom, it was assumed that the transect had been struck randomly. Path cross-overs and retreats on the transect which would cause repetitive surveying of the same bottom community were assumed to be infrequent. The order of entries on the tape was therefore assumed to represent a real sequence of epifauna.

Observations from a submersible present at least two problems. In the first case, identifications of fauna obviously cannot be confirmed. However, the observer had considerable experience in identification of organisms from this area (Caddy, 1970a). Secondly, the method of observation precludes information on very small epifauna and most infauna. While such an omission may represent a significant portion of the bottom community, macro-epifauna were recorded consistently. It was felt that this component of the bottom community was adequately observed during the submersible dives.

DATA ANALYSIS

The core of the statistical analysis of faunal adjacencies observed on the Digby scallop grounds was the sequence of entries of taxa on the recording tape. This represented a one-dimensional cross-sectional view of the bottom community. The relevant question was: do epifauna occur in random sequence or are there significant non-random (physically or biologically induced) adjacencies of fauna? Several analytical techniques have been developed to deal with the phenomenon of species contagion (e.g., Cole, 1946; Fager, 1957; Fager and Longhurst, 1968). However, Knight (1974) derived recursion formulae for probabilities and factorial moments for a run-like statistical treatment of one-dimensional transect data, with the present type of study in mind.

Before the data could be analysed, each observation had to be standardized to a common level. For example, taxonomic entries on the tape in some cases represented observations of individual organisms and in others represented observations of several individuals of one taxon at a time. For some organisms, such as hydroids, discrete individuals could not be defined. Because Knight's (1974) test cannot analyse self-adjacencies, it was felt that the concept of faunal patches (homogeneous for a given taxon) would standardise the data for

analysis, yet retain ecological significance. All entries were raised from the individual to the taxonomic level; for example, one sea anemone = three sea anemones = a discrete faunal patch. All faunal patches had equal weight in the mathematical analysis. Adjacencies of different taxa therefore were assumed to occur when one taxon (one individual or several) broke up the homogeneity of another taxon or when two different taxa occurred contiguously. In many cases, adjacencies in a heterogeneous bottom community are due to random processes and are tolerated by the individuals or faunal patches. On the other hand, significant adjacencies suggest an intrusion of one taxon into what would be a homogeneous faunal patch because of common bottom-type requirements or an association due to predation or commensalism.

Taxa which occur together less frequently than predicted by random processes (i.e., repulsion) probably have biological significance as well, although this phenomenon was not analyzed in the present study.

For each of the six dives, Knight's (1974) run-like statistic was applied to the data at $p \leq 0.05$. The statistic was also applied to observations from all the dives pooled together ($n_{\text{faunal patches}} = 869$). In the latter case, it was recognized that there were five artificial adjacencies accommodated in Knight's formulae because of discontinuities between subsets of data. However, these five adjacencies comprised such a small proportion of all possible adjacencies (<1%), that the discrepancy in the recursion formulae was ignored.

Because of the large number of adjacencies examined in each data set (up to 264 for all dives pooled together), a small number of random adjacencies could have been denoted as significant at $p \leq 0.05$. Two criteria were used to improve the screening of adjacencies. Adjacencies which were significant at $p \leq 0.05$ in at least half of the dives in which the adjacency was observed or in which the two taxa being considered were observed, but not adjacent, were denoted as statistically significant in this study. Adjacencies which were significant at $p \leq 0.05/n_{\text{tests}}$ (all dives pooled) were considered to be statistically significant as well.

Observations of cluckers (pairs of empty scallop valves) were eliminated from the sequence of faunal observations and only live organisms were considered. However, adjacencies of cluckers with live fauna were analyzed separately from the other data sets.

For brevity in tabulation, after the first reference, all taxa were denoted by their generic names only, except where there were two species per genus, or where identification to generic level was not possible.

RESULTS

Observations from the submersible indicated that the bottom in water depths from 82 to 107 m (Dives 1, 2 and 4) comprised hard clay overlain by gravel and shell fragments. These areas were crossed by low ridges of harder material such as small boulders and cobble. Fader *et al.* (1977) classified the sediments in this offshore area as Scotian Shelf drift; that is, poorly sorted cohesive till. A general sparsity of epifauna on the scallop grounds and the raked appearance of the loose sediments were almost certainly a result of commercial fishing (Caddy, 1973).

On the inshore grounds (Dives 5, 6 and 7), high-energy sedimentary structures were encountered. These commonly included sand waves up to 0.5 m in height, similar to structures observed on Georges Bank (Caddy and Iles, 1973). Step-like benches of coarse gravel, approximately 20 cm high and 1-2 m wide, were also encountered. These structures were populated by a low diversity fauna, consisting of *Polymastia* sp. on the sand waves and *Spisula* sp. on the gravel steps. Fader *et al.* (1977) classified sediments in this area as well-sorted Sambro sand, devoid of silt and clay-sized particles. The bottom types encountered along each transect are noted in Figs. 2-7 along with two-dimensional reconstructions of the observed epifaunal communities.

On almost all dives, dense layers of plankton, suspended particles, and streamers of organic material were observed throughout the water column, especially near the bottom. Visibility rarely exceeded three metres. On Dive 2, in approximately 100 m of water, chaetognaths and euphausiids were encountered near the bottom. Strong currents occurred on and near the bottom during almost all dives. The strength of the currents and the mobility of the smaller sediments indicated a high energy environment on the Digby scallop grounds.

Information on the number of taxa observed and density of faunal patches is shown in Table 1. The density of faunal patches was lowest on Snow Ground and Yankee Bank (Dives 1 and 2) and highest inshore of Yankee Bank (Dive 4). The density of faunal patches inshore (Dives 5, 6 and 7) was remarkably constant (Table 1).

Fifty-two taxa were observed on or near the bottom; 33 of these were observed during Dive 2 at the deepest station. Table 2 shows the locations of observations of each taxon. The percentage frequency of observation of each taxon is noted in Fig. 8. Sea anemones were the most frequently observed faunal patches (Fig. 8). Scallops (*Placopecten magellanicus*) and hermit crabs (*Pagurus* sp.) were the next most frequently observed fauna. *Pagurus* sp. were more common inshore than offshore.

Sponges were relatively common throughout the scallop grounds. *Polymastia* sp. in particular favoured the shallower inshore locations, and appeared to survive the migration of sand waves by extended growth of the fingerlike projections. Sea anemones and hydroids were observed in all locations. Sea anemones favoured rocks while the hydroids formed dense mats over gravel and on scallop shells. Alcyonarians (probably *Gersemia* sp.) were observed only during Dive 5 inshore. Brachiopods (*Terebratulina septentrionalis*) were very common in the deeper areas of Yankee Bank and absent from inshore locations. Whelks were the most frequently observed gastropods, *Neptunea decemcostata* being the most common. Whelks occurred throughout the scallop grounds. The most frequently observed bivalve was the scallop which predominated in deeper gravel areas. Surf clams (*Spisula* sp.) tended to replace scallops in the inshore sandy areas. Tubiculous polychaete worms, especially *Pilograna* sp., were observed throughout the scallop grounds, and formed distinct reefs in the Yankee Bank area.

The barnacle, *Balanus balanus* was very common, especially on scallop shells. *Balanus haneri* was restricted to the deeper water of Yankee Bank. Only one lobster was observed in the inshore area.

A relatively large number of echinoderms occurred throughout the scallop grounds. *Solaster endeca* and *Henricia* sp. were the most common. *Hippasteria phrygiana*, *S. papposus* and *Pteraster militaris* were restricted to offshore locations while *Asterias vulgaris* only occurred inshore. Sea urchins were not abundant.

The urochordate, *Boltenia* sp., was frequently observed on the scallop grounds, but appeared to favour the offshore areas. Hagfish (*Myxine glutinosa*) and gadids (mostly pollock) were the most frequently observed fish. While the gadids occurred throughout the area, hagfish were only seen on or near Yankee Bank. Skates, alligatorfish, and redfish were restricted to the offshore area. Sculpins, stichaeids, and zoarcids (eel pouts) occurred sporadically throughout the survey area. Pholids occurred inshore.

Several epifauna showed an apparently high frequency of self-contagion. Sea anemones, sponges, and serpulid worms especially showed a high degree of clumping of individuals. *Solaster endeca*, *Henricia* and whelks were frequently clumped as well.

Tables 3 to 16 show the specific details of faunal adjacencies noted on each dive and for all dives pooled together. These data are summarized in Table 17. Adjacencies which were screened by the two criteria noted previously are listed in Table 18, along with classification by feeding type.

After screening, there were 26 faunal adjacencies which were statistically significant. Sixteen of the adjacencies included a predator and an animal with a different feeding mode (Table 18). Two adjacencies between potential predators (*Pagurus* and pholid; *Hippasteria* and *Pteraster*) were significant. There were six significant adjacencies between suspension feeders, one between a suspension feeder and a surface detritivore, and one between a suspension feeder and a scavenger (Table 18).

Table 19 shows the adjacencies between scallop cluckers and fauna. As expected, the adjacency of cluckers with live scallops was significant. Pholids showed a significant adjacency with scallop cluckers as well.

DISCUSSION

Grab sampling by Wagner (1979) and Peer *et al.* (1980) within and near the present study area reflected the difficulty with quantitative sampling of relatively hard sediments. Most of the samples collected by Peer *et al.* (1980) in the study area were non-quantitative because of incomplete closure of the grab. However, they observed relatively high densities of *Dentalium* and *Terebratulina* at stations 74 and 75, near the sites of Dives 2 and 4 in this study. These observations concur with the dive observations in the deeper habitat. Peer *et al.* (1980) also observed a relatively diverse infauna near the site of Dive 2, corresponding to a relatively diverse epifauna noted in this study. The deeper offshore habitat appears to be conducive to colonization by both infauna and epifauna, reflecting the admixture of coarse material with clay-sized particles.

The infrequent occurrence of epifauna in grabs (Peer *et al.*, 1980) from the study area reconfirmed the importance of dredging, photography, and direct observation of the epifaunal community.

The observations from the submersible confirmed the distributions of epifauna on the Digby scallop grounds recorded by Caddy (1970a), with a few notable exceptions. Caddy (1970a) collected few sea anemones, hermit crabs, *Boltenia* sp., *Henricia* sp., and *Pteraster militaris* within the present study area. However, observations from the submersible indicated that these organisms comprised a significant part of the epifaunal community in the study area. Although a shift in epifaunal distribution could have occurred between 1966 and 1969 to account for the apparent disparities in the studies, ineffectiveness of the dredge in collecting certain epifaunal taxa on particularly rough bottom is more likely the cause. These differences between the two studies confirm earlier strong suspicions that significant bias may result from interpretation of the epifauna from dredge sampling alone.

Because submersibles permit non-destructive observation of deep epifaunal communities, real spatial associations between different taxa can be recorded. Such observations, combined with a rigourous run-like statistic (Knight, 1974), can indicate potential functional relationships between faunal taxa.

Considering the 52 faunal taxa observed on the Digby scallop grounds, 1,326 different faunal adjacencies could have been observed if all taxa were adjacent to all other taxa at least once. In fact, 264 different faunal adjacencies were observed. Of these, 64 were significant at $p \leq 0.05$ on at least one dive, if not more, and only 26 (less than 10%), passing the criteria indicated previously, possibly reflected a functional relationship between faunal taxa.

Of the 31 potentially significant adjacencies which could occur between 15 of the constituent species in the assemblages described by Caddy (1970a), and which were also observed in this study, only two were significant: barnacles (*Balanus balanus*) and scallops, and the adjacency of *Hippasteria phrygiana* with sponges (*Haliclona*). This reiterates that the common presence of most species within a habitat is related to the physical characteristics of the habitat. The distribution of most epifaunal species in relation to other faunal species is random. Only a few epifaunal species show a distribution which is closely related to one other species, implying a functional relationship.

Eighteen of the 26 significant adjacencies involved predators and therefore may have reflected predator-prey relationships in the study area. Unfortunately, documentation of benthic feeding types is poor (Maurer *et al.*, 1979), and little can be said about these adjacencies without gut content analysis. However, at least one of these adjacencies is well documented. The observed adjacency of *Calliostoma* with alcyonarians (probably *Gersemia* sp.) reflects the well-known preference of this gastropod for alcyonarians (Perron and Turner, 1978).

The adjacencies of sponges with horse mussels and barnacles with scallops may reflect provision of substrate to the smaller suspension feeders and benefit from an increased supply of suspended nutrients generated by the inhalent current of the host (Forester, 1979). Sponges may interfere with attachment of asteroid tube feet on bivalves (Forester, 1979), and therefore provide some protection to the host. It is not clear if barnacles provide any benefit to scallops.

Pholids showed a significant adjacency with scallop cluckers. This may indicate use of the valves as shelter. Blennioid fish on the Nova Scotia coast have been observed living in scallop cluckers (Carter, unpublished data), and squirrel hake (*Urophycis chuss*) sometimes occur in live scallops (Leim and Scott, 1966).

The significant adjacency of scallops and surf clams on the Digby grounds was due to high frequency of co-occurrence at the shallowest station (Dive 5). Normally, scallops and surf clams would be expected to have discrete centres of distribution (Caddy, 1970a); however, overlap zones must occur. The region of Dive 5 may be an overlap zone between the scallop and surf clam communities.

Adjacencies between alcyonarians and *Potamilla*, hydroids and serpulids, and *Potamilla* and *Boltenia* (all suspension feeders) may reflect common, but specific, requirements of the physical environment, such as bottom type, current regime, and height off sea bottom.

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TABLE 1. Dive Information.

	Dive 1	Dive 2	Dive 4	Dive 5	Dive 6	Dive 7
Date:	10/09/69	11/09/69	12/09/69	12/09/69	13/09/69	13/09/69
Location:	Snow Ground	Yankee Bank	Inshore of Yankee Bank	Inshore	Broad Cove Ground	Buoy Ground
Observer:	J.F. Caddy	J.F. Caddy	J.F. Caddy	J.F. Caddy	J.F. Caddy	J.F. Caddy
Heading used for epifaunal observations:	060°	215° (8 min) 125° (30 min) 215° (9 min) 224° (8 min)	248° (11 min) 210° (11 min) 240° (18 min)	090°	235° (9 min) 250° (4 min) 255° (2 min)	246° (12 min) 060° (18 min)
Duration of observations (min):	28	55	40	16	15	30
Number of odometer revolutions	155	177 for 26 min	165	74	35	75 for 16 min
Distance travelled over bottom (m):	296	estimated - 715	315	141	67	estimated - 268
Mean odometer speed (m/min):	10.5	13	7.9	8.8	4.5	8.9
Range of depth of submersible along transect (m):	82.0 - 86.3	103.9 - 106.7	86.9 - 91.4	74.7	83.8 - 91.4	81.4 - 91.7
General bottom type:	hard bottom with shell, small rocks, boulders	muddy gravel and shell with small rocks	rough ridged bottom with shell, gravel, and larger rocks	ridged gravel, sand, and shell with some rocks	undulating gravel, shell, and sand with distinct ridges and some rocks	sandy gravel with shells and small rocks, occasionally ridged
Number of taxa observed:	22	33	28	20	13	28
Number of individual faunal patches:	101	305	205	76	36	146
Number of faunal patches/100 m:	34	43	65	54	54	55

TABLE 2. Fauna observed during submersible dives on the scallop grounds off Digby, Nova Scotia (September 10-13, 1969).

Taxon	Symbol	Dives during which fauna observed
Porifera		
Haliclona sp.		1,4,7
Polymastia sp.		1,5,6,7
Trichostemma hemisphericum (M. Sars)		1,2,4,5,7
unidentified sponges		1,2,4,6,7
Cnidaria		
alcyonarian		5
sea anemone		1,2,4,5,6,7
epifaunal hydroids		1,2,4,5,6,7
Tubularia sp.		6
Bryozoa		
Flustra sp.		1
Brachiopoda		
Terebratulina septentrionalis (Couthouy)		2,4
Mollusca		
Gastropoda		
Calliostoma sp.		4,5,7
Polinices heros Say 1822		7
Buccinum undatum L. 1761		1,2,4,5,6,7
Neptunea decemcostata Say 1826		1,2,4,5,7
Colus stimpsoni Moerch 1867		1,2,4,5,7
Aeolidia papillosa L. 1761		2

TABLE 2 (Continued). Fauna observed during submersible dives on the scallop grounds off Digby, Nova Scotia (September 10-13, 1969).

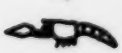
Taxon	Symbol	Dives during which fauna observed
Mollusca (Continued)		
Scaphopoda		
Dentalium entale L. 1758		2
Pelecypoda		
Modiolus modiolus L. 1758		2,4
Placopecten magellanicus Gmelin		1,2,4,5,6,7
Astarte sp.		2
Cardita borealis Conrad 1831		7
Arctica islandica L. 1758		1
Cerastoderma pinnulatum Conrad 1831		2
Clinocardium ciliatum Fabricius 1780		2
Spisula sp.		5,6,7
Ensis directus Conrad 1843		7
Annelida		
Potamilla sp.		2,5,6
serpulid worm		2
Filograna implexa Berkeley 1851		1,2,4,5,7
Arthropoda		
Crustacea		
Balanus balanus (L.) 1758		2,4,5,7
B. hameri (Ascanius) 1761		2,4
Pandalus sp.		4
Homarus americanus Milne-Edwards 1837		7
Pagurus sp.		1,2,4,5,6,7

TABLE 2 (Continued). Fauna observed during submersible dives on the scallop grounds off Digby, Nova Scotia (September 10-13, 1969).

Taxon	Symbol	Dives during which fauna observed
Echinodermata		
Psolus sp.		2
Strongylocentrotus droebachiensis (Muller) 1776		1,7
Hippasteria phrygiana (Parelius) 1770		2,4
Solaster endeca (L.)		1,2,4,5,6,7
Solaster papposus (L.) 1780		1,2,4
Pteraster militaris (Muller) 1776		1,2,4
Henricia sp.		1,2,4,5,6,7
Asterias vulgaris Verrill 1866		7
Leptasterias sp.		1
Chordata		
Urochordata		
Boltenia sp.		2,4,7
Pisces		
Myxine glutinosa L. 1758		2,4
Raja sp.		2,4
gadid fish		1,4,5,6,7
pholid fish		5,7
stichaeid and zoarcid fish		2,4,5,7
Sebastes marinus (L.) 1758		4
Myoxocephalus sp.		1,2,7
Aspidophoroides monopterygius (Bloch) 1786		2

TABLE 3. Numbers of adjacencies of fauna observed on Dive 1 (n = 101).

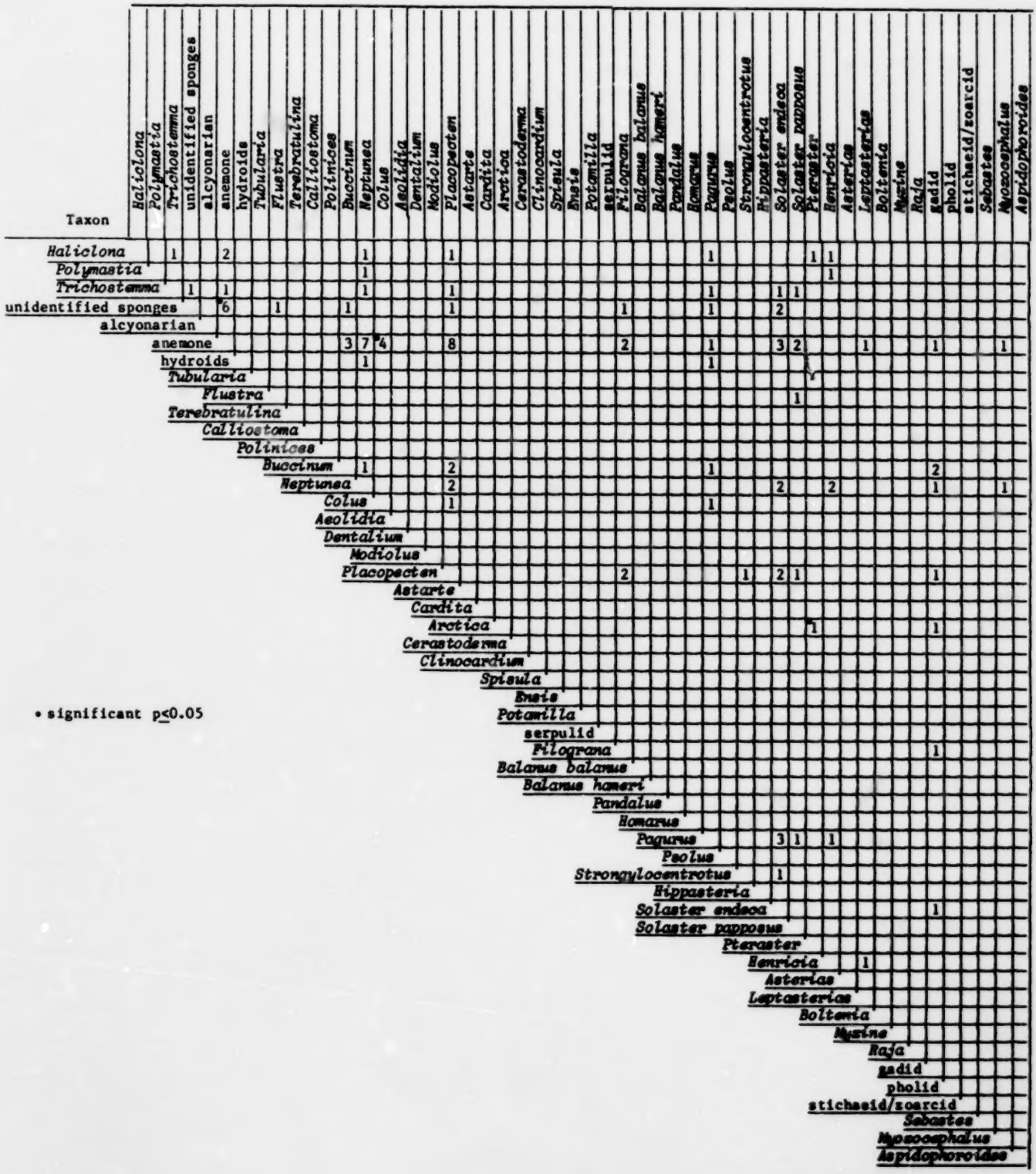


TABLE 4. Numbers of adjacencies of fauna observed on Dive 2 (n = 305).

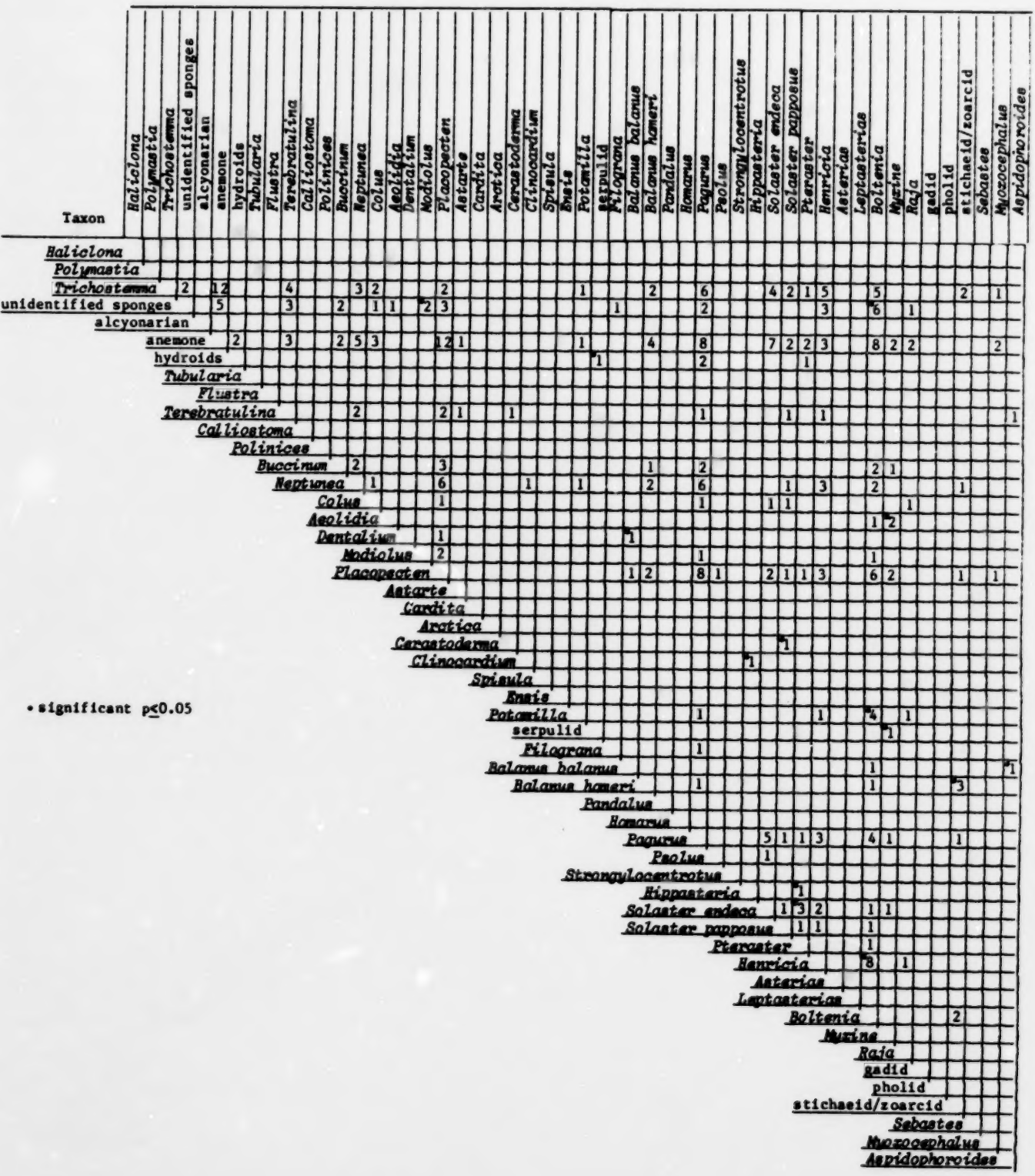


TABLE 5. Numbers of adjacencies of fauna observed on Dive 4 (n = 205).

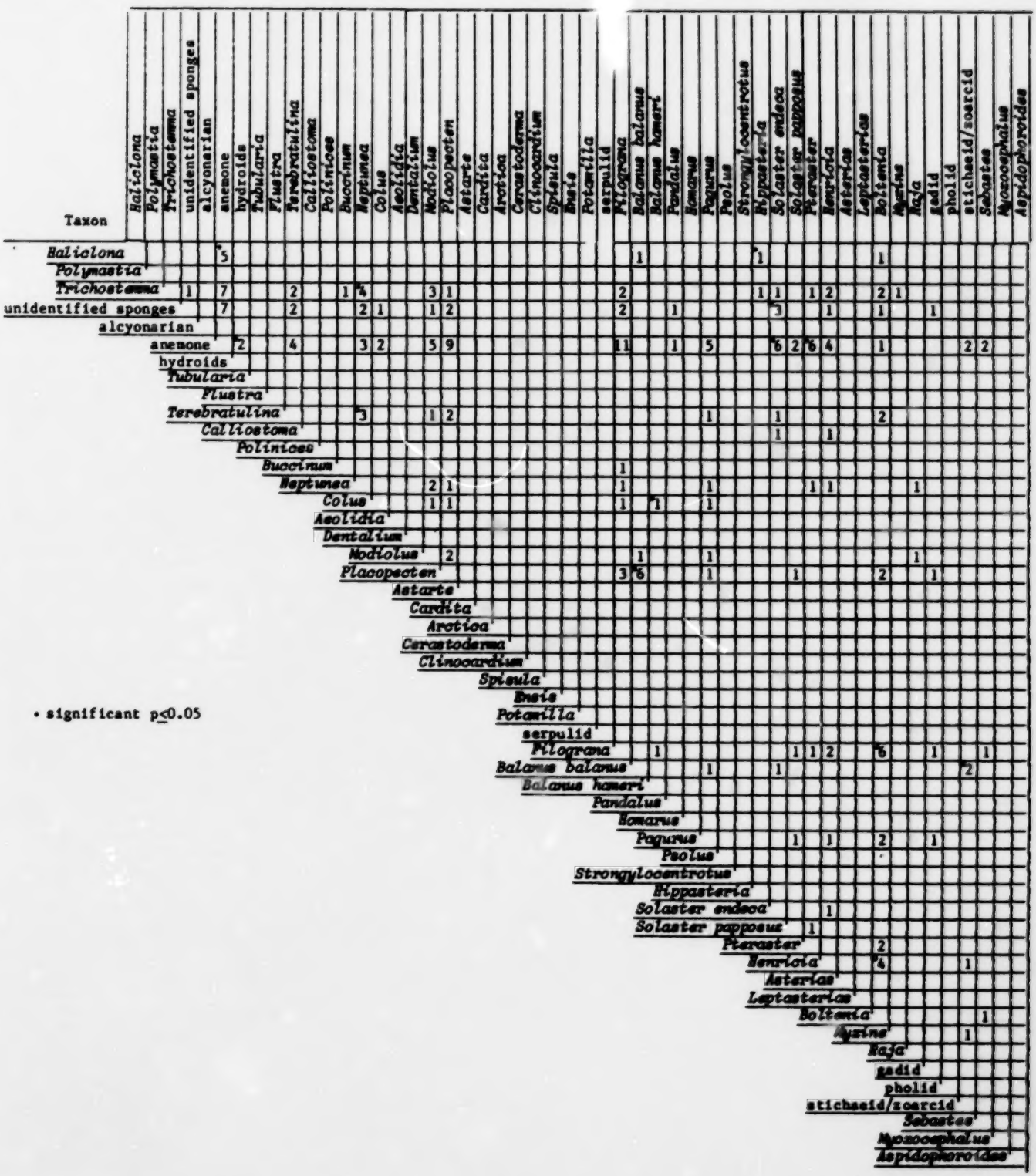


TABLE 6. Numbers of adjacencies of fauna observed on Dive 5 (n = 76).

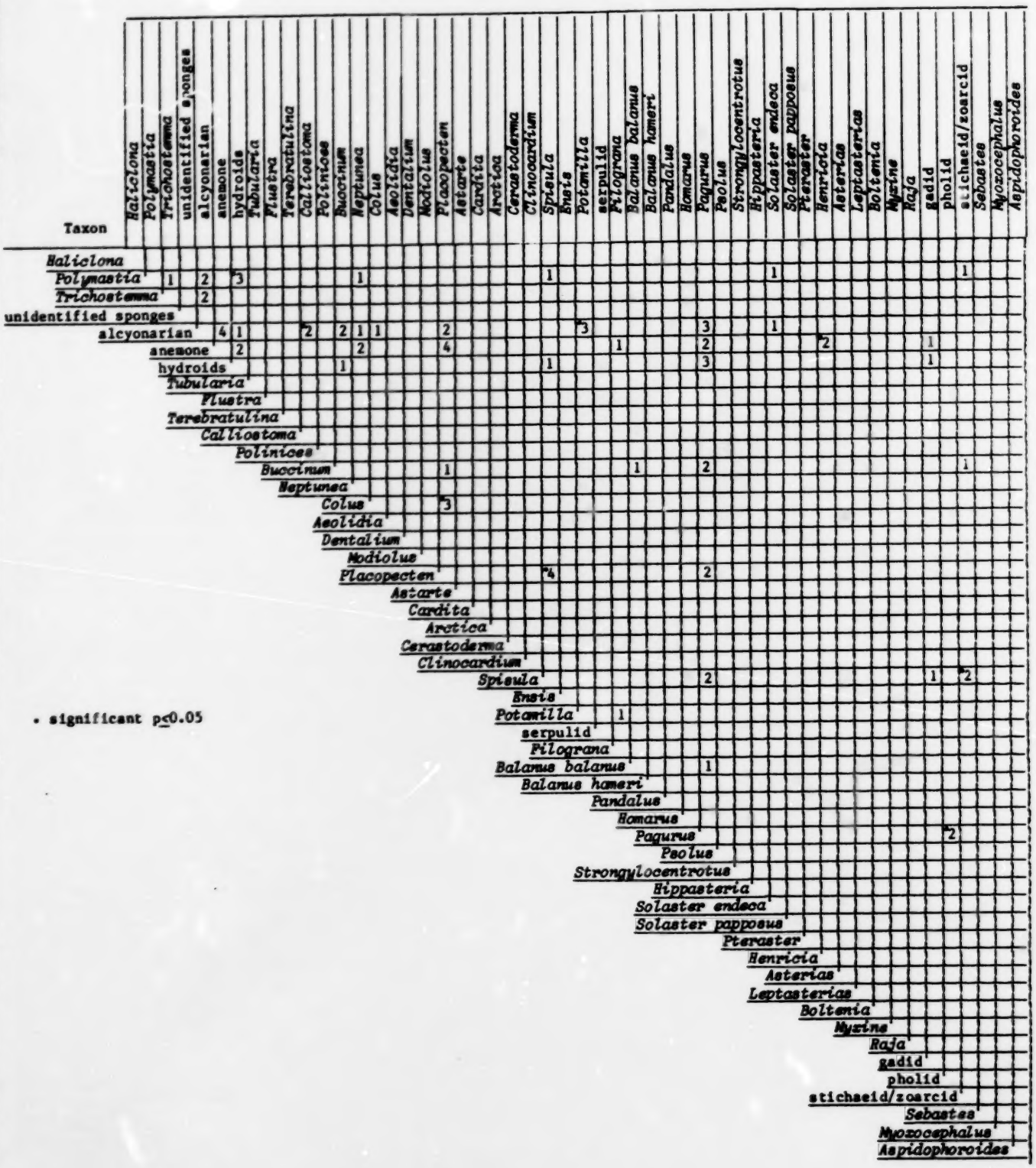


TABLE 7. Numbers of adjacencies of fauna observed on Dive 6 (n = 36).

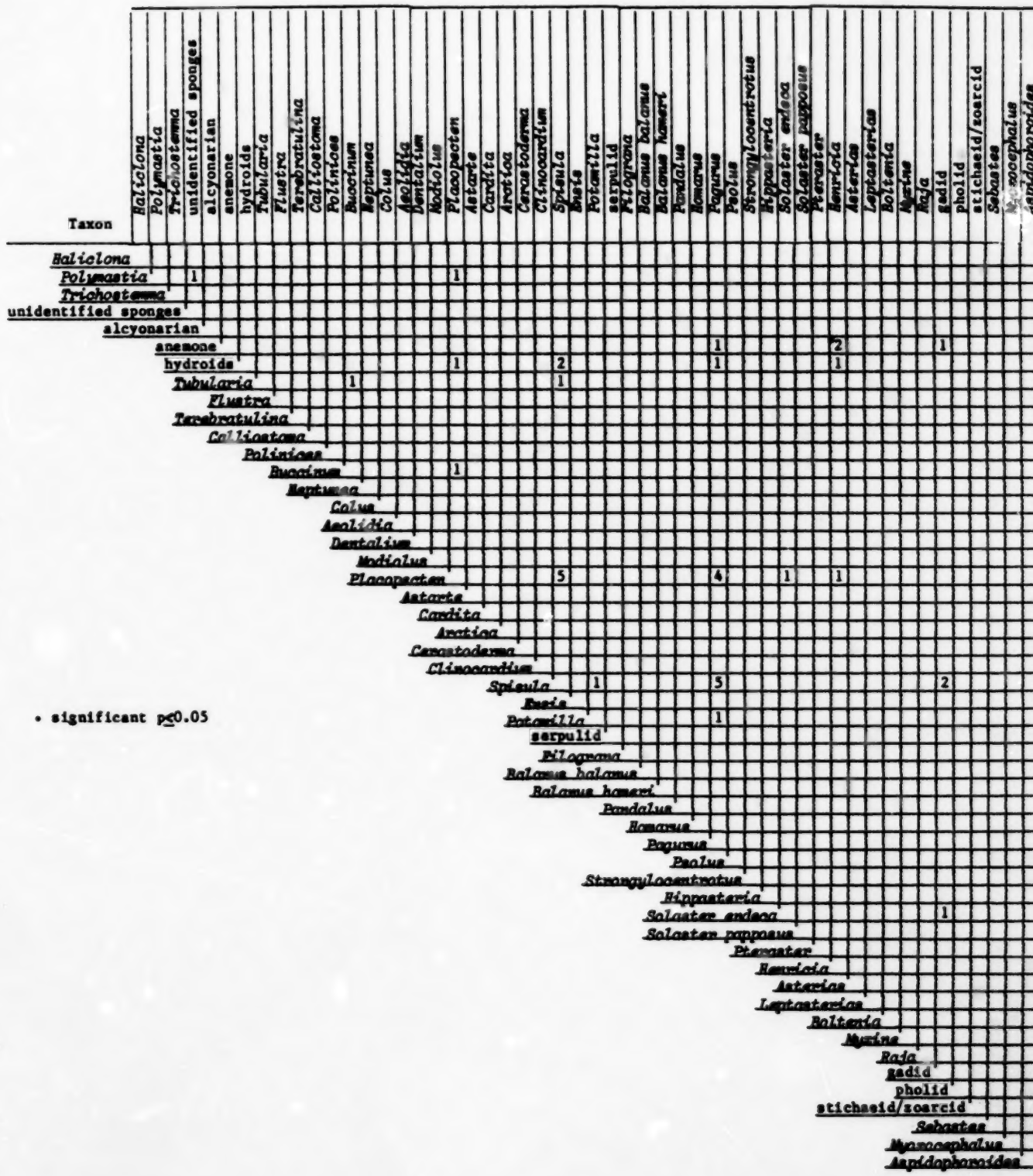


TABLE 8. Numbers of adjacencies of fauna observed on Dive 7 (n = 146).

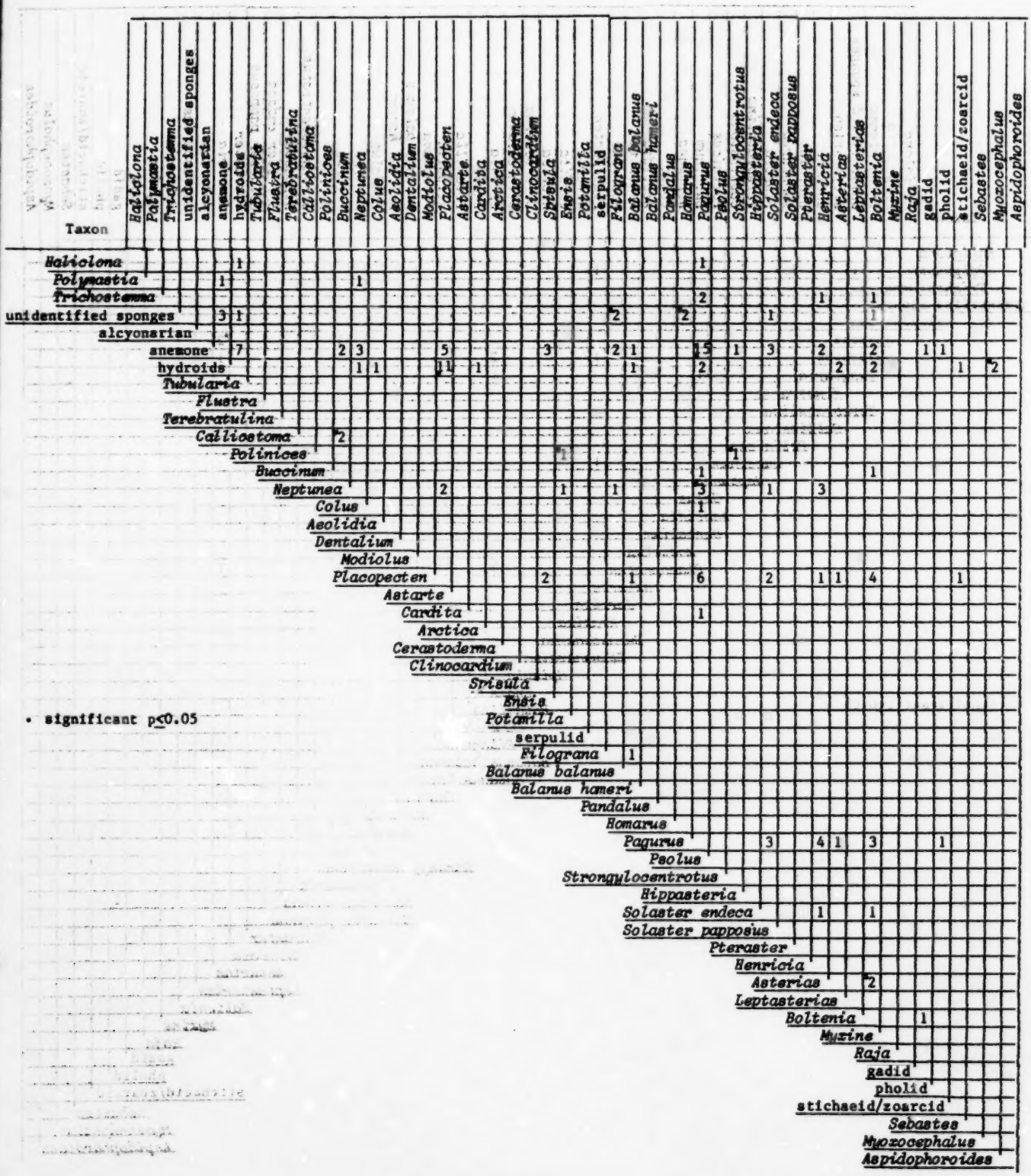


TABLE 9. Numbers of adjacencies of fauna observed on all dives (n = 869).

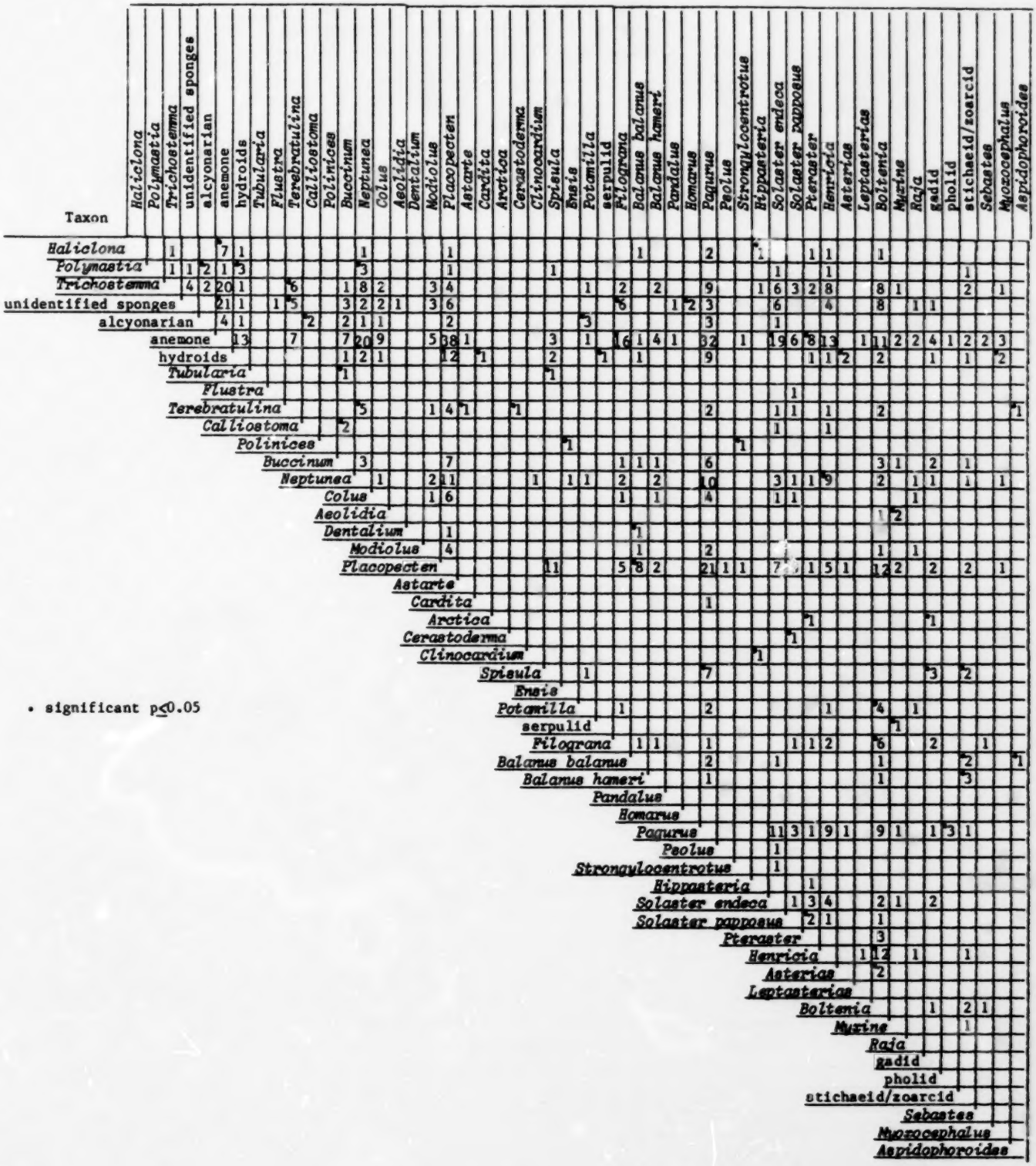


TABLE 10. Summary of occurrences of faunal patches on Dive 1 (n = 101).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona	4	4	7
Polymastia	1	1	2
Trichostemma	4	4	8
unidentified sponges	7	7	8
alcyonarian			
anemone	21	21	14
hydroids	1	1	2
Tubularia			
Flustra	1	1	2
Terebratulina			
Calliostoma			
Polinices			
Buccinum	5	5	6
Neptunea	10	10	11
Colus	3	3	3
Aeolidia			
Dentalium			
Modiolus			
Placopecten	12	12	12
Astarte			
Cardita			
Arctica	1	1	2
Cerastoderma			
Clinocardium			
Spisula			
Ensis			
Potamilla			
serpulid			
Filograna	3	3	4
Balanus balanus			
Balanus hameri			
Pandalus			
Homarus			
Pagurus	6	6	10
Psolus			
Strongylocentrotus	1	1	2
Hippasteria			
Solaster endeca	8	8	8
Solaster papposus	3	3	5
Pteraster	1	1	2
Henricia	3	3	5
Asterias			
Leptasterias	1	1	2
Boltenia			
Myxine			
Raja			
gadid	4	4	7
pholid			
stichaeid/zoarcid			
Sebastes			
Myoxocephalus	1	1	2
Aspidophoroides			

TABLE 11. Summary of occurrences of faunal patches on Dive 2 (n = 305).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona			
Polymastia			
Trichostemma	27	9	16
unidentified sponges	16	5	13
alcyonarian			
anemone	43	14	20
hydroids	3	1	4
Tubularia			
Flustra			
Terebratulina	10	3	11
Calliostoma			
Polinices			
Buccinum	8	3	8
Neptunea	18	6	14
Colus	6	2	8
Aeolidia	2	0.7	3
Dentalium	1	0.3	2
Modiolus	3	1	4
Placopecten	31	10	21
Astarte	1	0.3	2
Cardita			
Arctica			
Cerastoderma	1	0.3	2
Clinocardium	1	0.3	2
Spisula			
Ensis			
Potamilla	5	2	7
serpulid	1	0.3	2
Filograna	1	0.3	2
Balanus balanus	2	0.7	4
Balanus hameri	8	3	8
Pandalus			
Homarus			
Pagurus	28	9	20
Psolus	1	0.3	2
Strongylocentrotus			
Hippasteria	1	0.3	2
Solaster endeca	14	5	11
Solaster papposus	7	2	12
Pteraster	6	2	9
Henricia	17	6	12
Asterias			
Leptasterias			
Boltenia	27	9	17
Myxine	5	2	7
Raja	3	1	5
gadid			
pholid			
stichaeid/zoarcid	5	2	6
Sebastes			
Myoxocephalus	2	0.7	3
Aspidophoroides	1	0.3	2

TABLE 12. Summary of occurrences of faunal patches on Dive 4 (n = 205).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona	4	2	4
Polymastia			
Trichostemma	15	7	14
unidentified sponges	13	6	13
alcyonarian			
anemone	42	20	19
hydroids	1	0.5	1
Tubularia			
Flustra			
Terebratulina	9	4	9
Calliostoma	1	0.5	2
Polinices			
Buccinum	1	0.5	2
Neptunea	10	5	11
Colus	4	2	7
Aeolidia			
Dentalium			
Modiolus	9	4	10
Placopecten	16	8	13
Astarte			
Cardita			
Arctica			
Cerastoderma			
Clinocardium			
Spisula			
Ensis			
Potamilla			
serpulid			
Filograna	17	8	14
Balanus balanus	6	3	6
Balanus hameri	1	0.5	2
Pandalus	1	0.5	2
Homarus			
Pagurus	8	4	11
Psolus			
Strongylocentrotus			
Hippasteria	1	0.5	2
Solaster endeca	7	3	7
Solaster papposus	3	1	5
Pteraster	6	3	6
Henricia	9	4	10
Asterias			
Leptasterias			
Boltenia	12	6	11
Myxine	1	0.5	2
Raja	1	0.5	2
gadid	2	1	4
pholid			
stichaeid/zoarcid	3	1	4
Sebastes	2	1	3
Myoxocephalus			
Aspidophoroides			

TABLE 13. Summary of occurrences of faunal patches on Dive 5 (n = 76).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona			
Polymastia	5	7	7
Trichostemma	2	3	3
unidentified sponges			
alcyonarian	12	16	12
anemone	9	12	8
hydroids	6	8	7
Tubularia			
Flustra			
Terebratulina			
Calliostoma	1	1	1
Polinices			
Buccinum	4	5	6
Neptunea	2	3	3
Colus	2	3	2
Aeolidia			
Dentalium			
Modiolus			
Placopecten	8	11	6
Astarte			
Cardita			
Arctica			
Cerastoderma			
Clinocardium			
Spisula	5	7	5
Ensis			
Potamilla	2	3	2
serpulid			
Filograna	1	1	2
Balanus balanus	1	1	2
Balanus hameri			
Pandalus			
Homarus			
Pagurus	9	12	8
Psolus			
Strongylocentrotus			
Hippasteria			
Solaster endeca	1	1	2
Solaster papposus			
Pteraster			
Henricia	1	1	1
Asterias			
Leptasterias			
Boltenia			
Myxine			
Raja			
gadid	2	3	3
pholid	1	1	1
stichaeid/zoarcid	2	3	3
Sebastes			
Myoxocephalus			
Aspidophoroides			

TABLE 14. Summary of occurrences of faunal patches on Dive 6 (n = 36).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona			
Polymastia	1	3	2
Trichostemma			
unidentified sponges	1	3	1
alcyonarian			
anemone	2	6	3
hydroids	3	8	4
Tubularia	1	3	2
Flustra			
Terebratulina			
Calliostoma			
Polinices			
Buccinum	1	3	2
Neptunea			
Colus			
Aeolidia			
Dentalium			
Modiolus			
Placopecten	7	19	7
Astarte			
Cardita			
Arctica			
Cerastoderma			
Clinocardium			
Spisula	8	22	6
Ensis			
Potamilla	1	3	2
serpulid			
Filograna			
Balanus balanus			
Balanus hameri			
Pandalus			
Homarus			
Pagurus	6	17	5
Psolus			
Strongylocentrotus			
Hippasteria			
Solaster endeca	1	3	2
Solaster papposus			
Pteraster			
Henricia	2	6	3
Asterias			
Leptasterias			
Boltenia			
Myxine			
Raja			
gadid	2	6	3
pholid			
stichaeid/zoarcid			
Sebastes			
Myoxocephalus			
Aspidophoroides			

TABLE 15. Summary of occurrences of faunal patches on Dive 7 (n = 146).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona	1	0.7	2
Polymastia	1	0.7	2
Trichostemma	2	1	3
unidentified sponges	5	3	6
alcyonarian			
anemone	26	18	16
hydroids	17	12	13
Tubularia			
Flustra			
Terebratulina			
Calliostoma	1	0.7	2
Polinices	1	0.7	2
Buccinum	3	2	4
Neptunea	8	5	9
Colus	1	0.7	2
Aeolidia			
Dentalium			
Modiolus			
Placopecten	18	12	11
Astarte			
Cardita	1	0.7	2
Arctica			
Cerastoderma			
Clinocardium			
Spisula	3	2	2
Ensis	1	0.7	2
Potamilla			
serpulid			
Filograna	3	2	4
Balanus balanus	2	1	4
Balanus hameri			
Pandalus			
Homarus	1	0.7	1
Pagurus	22	15	14
Psolus			
Strongylocentrotus	1	0.7	2
Hippasteria			
Solaster endeca	6	4	7
Solaster papposus			
Pteraster			
Henricia	6	4	6
Asterias	3	2	4
Leptasterias			
Boltenia	9	6	10
Myxine			
Raja			
gadid	1	0.7	2
pholid	1	0.7	2
stichaeid/zoarcid	1	0.7	2
Sebastes			
Myoxocephalus	1	0.7	1
Aspidophoroides			

TABLE 16. Summary of occurrences of faunal patches on all dives (n = 869).

Taxon	Number of individual patches/taxon	% of all observed faunal patches	Number of taxa to which adjacent
Haliclona	9	1	11
Polymastia	8	1	11
Trichostemma	50	6	25
unidentified sponges	42	5	21
alcyonarian	12	1	12
anemone	143	16	34
hydroids	31	4	22
Tubularia	1	0.1	2
Flustra	1	0.1	2
Terebratulina	19	2	14
Calliostoma	3	0.3	4
Polinices	1	0.1	2
Buccinum	22	3	17
Neptunea	48	6	27
Colus	16	2	14
Aeolidia	2	0.2	3
Dentalium	1	0.1	2
Modiolus	12	1	11
Placopecten	92	11	30
Astarte	1	0.1	2
Cardita	1	0.1	2
Arctica	1	0.1	2
Cerastoderma	1	0.1	2
Clinocardium	1	0.1	2
Spisula	16	2	9
Ensis	1	0.1	2
Potamilla	8	1	10
serpulid	1	0.1	2
Filograna	25	3	17
Balanus balanus	11	1	13
Balanus hameri	9	1	10
Pandalus	1	0.1	2
Homarus	1	0.1	1
Pagurus	79	9	28
Psolus	1	0.1	2
Strongylocentrotus	2	0.2	4
Hippasteria	2	0.2	4
Solaster endeca	37	4	20
Solaster papposus	13	1	14
Pteraster	13	1	13
Henricia	38	4	19
Asterias	3	0.3	4
Leptasterias	1	0.1	2
Boltenia	48	6	24
Myxine	6	1	9
Raja	4	0.5	7
gadid	11	1	12
pholid	2	0.2	2
stichaeid/zoarcid	11	1	14
Sebastes	2	0.2	3
Myoxocephalus	4	0.5	5
Aspidophoroides	1	0.1	2

TABLE 17. Summary of faunal adjacencies observed on the Digby scallop grounds.

Adjacency	Dive Number 1	2	4	5	6	7	All dives pooled
Haliclona - anemone	–		*			.	*
Haliclona - *Hippasteria*			*				*
Polymastia - alcyonarian				–			*
Polymastia - hydroids	.			*	.	.	*
Polymastia - *Neptunea*	–			–		–	*
Trichostemma - *Terebratulina*		–	–				*
Trichostemma - *Neptunea*	–	–	*	.		.	
unidentified sponges - anemone	*	–	–		.	–	*
unidentified sponges - *Terebratulina*		–	–				*
unidentified sponges - *Modiolus*		*	–				
unidentified sponges - *Filograna*	–	–	–			*	*
unidentified sponges - *Homarus*						*	**
unidentified sponges - *Solaster endeca*	–	.	*		.	–	
unidentified sponges - *Boltenia*		*	–			–	
alcyonarian - *Calliostoma*				*			**
alcyonarian - *Potamilla*				*			**
anemone - hydroids	.	–	*	–	.	–	
anemone - *Colus*	*	–	–	.		.	
anemone - *Filograna*	–	.	–	–		–	*
anemone - *Pagurus*	–	–	–	–	–	*	
anemone - *Solaster endeca*	–	–	*	.	.	–	*
anemone - *Pteraster*	.	–	*				*
anemone - *Henricia*	.	–	–	*	*	–	
hydroids - *Placopecten*	.	.	.	.	–	*	*
hydroids - *Cardita*						–	*
hydroids - serpulid		*					*
hydroids - *Asterias*						–	*
hydroids - *Myoxocephalus*	.	.				*	*
Tubularia - *Buccinum*					–		*
Tubularia - *Spisula*					–		*
Terebratulina - *Neptunea*		–	*				
Terebratulina - *Astarte*		–					*
Terebratulina - *Cerastoderma*		–					*
Terebratulina - *Aspidophoroides*		–					*
Calliostoma - *Buccinum*			.	.		*	*
Polinices - *Ensis*						*	*
Polinices - *Strongylocentrotus*						*	*
Neptunea - *Pagurus*	.	–	–	.		*	
Neptunea - *Henricia*	–	–	–	.		–	*
Colus - *Placopecten*	–	–	–	*		.	
Colus - *Balanus hameri*		.	*				
Aeolidia - *Myxine*		*					*
Dentalium - *Balanus balanus*		*					*
Placopecten - *Spisula*				*	–	–	**
Placopecten - *Balanus balanus*	–	–	*	.		–	**
Arctica - *Pteraster*	*						*
Arctica - gadid	–						*
Cerastoderma - *Solaster papposus*		*					*
Clinocardium - *Hippasteria*		*					*
Spisula - *Pagurus*				–	–	.	*
Spisula - gadid				–	–	.	*
Spisula - stichaeid/zoarcid				*		.	*

TABLE 17 (Continued). Summary of faunal adjacencies observed on the Digby scallop grounds.

Adjacency	Dive Number 1	2	4	5	6	7	All dives pooled
Potamilla - Boltenia		*					*
serpulid - *Myxine*		*					*
Filograna - Boltenia		.	*			.	*
Balanus balanus - stichaeid/zoarcid		.	*	.		.	*
Balanus balanus - Aspidophoroides		*					*
Balanus hameri - stichaeid/zoarcid		*	.				**
Pagurus - pholid				*		-	**
Hippasteria - Pteraster		*	.				
Solaster endeca - Pteraster	.	*	.				
Solaster papposus - Pteraster	.	-	-				*
Henricia - Boltenia		*	*			.	**
Asterias - Boltenia						*	*

* significant at $p \leq 0.05$

** significant at $p \leq 0.05/n_{tests}$ (all dives pooled)

. both taxa present but not adjacent

\- adjacency observed but not significant

TABLE 18. Summary of statistically significant adjacencies (see Materials and Methods) on the Digby scallop grounds.

Adjacency	Expressed as feeding types
Haliclona - *Hippasteria*	suspension feeder - predator
unidentified sponges - *Modiolus*	suspension feeder - suspension feeder
unidentified sponges - *Homarus*	suspension feeder - predator
alcyonarian - *Calliostoma*	suspension feeder - predator
alcyonarian - *Potamilla*	suspension feeder - suspension feeder
hydroids - serpulid	suspension feeder - suspension feeder
Terebratulina - *Neptunea*	suspension feeder - predator
Polinices - *Ensis*	predator - suspension feeder
Polinices - *Strongylocentrotus*	predator - grazer
Colus - *Balanus hameri*	predator - suspension feeder
Aeolidia - *Myxine*	predator - scavenger
Dentalium - *Balanus balanus*	surface detritivore - suspension feeder
Placopecten - *Spisula*	suspension feeder - suspension feeder
Placopecten - *Balanus balanus*	suspension feeder - suspension feeder
Arctica - *Pteraster*	suspension feeder - predator
Cerastoderma - *Solaster papposus*	suspension feeder - predator
Clinocardium - *Hippasteria*	suspension feeder - predator
Spisula - stichaeid/zoarcid	suspension feeder - predator
Potamilla - *Boltenia*	suspension feeder - suspension feeder
serpulid - *Myxine*	suspension feeder - scavenger
Balanus balanus - *Aspidophoroides*	suspension feeder - predator
Balanus hameri - stichaeid/zoarcid	suspension feeder - predator
Pagurus - pholid	predator/detritivore - predator
Hippasteria - *Pteraster*	predator - predator
Henricia - *Boltenia*	predator/suspension feeder - suspension feeder
Asterias - *Boltenia*	predator - suspension feeder

TABLE 19. Adjacencies of cluckers (pairs of empty scallop valves) with fauna on the Digby scallop grounds.

Taxon	
anemone	48
Placopecten	56*
Pagurus	28
Trichostemma	11
Neptunea	16
Boltenia	20
unidentified sponges	11
hydroids	12
Solaster endeca	11
Henricia	8
Buccinum	3
Filograna	7
Terebratulina	5
Colus	6
Spisula	7
Haliclona	2
Polymastia	2
alcyonarian	4
Modiolus	3
Potamilla	4
Balanus balanus	3
Balanus hameri	3
Solaster papposus	6
Pteraster	3
Myxine	2
gadid	2
stichaeid/zoarcid	3
Raja	-
Myoxocephalus	1
Calliostoma	-
Asterias	-
Aeolidia	2
Strongylocentrotus	1
Hippasteria	-
pholid	3*
Sebastes	-
Tubularia	-
Flustra	-
Polinices	1
Dentalium	-
Astarte	-
Cardita	1
Arctica	1
Cerastoderma	1
Clinocardium	1
Ensis	1
serpulid	1
Pandalus	1
Homarus	-
Psolus	-
Leptasterias	-
Aspidophoroides	-

* significant adjacency at $p \leq 0.05$ (Knight, 1974) n = 151 cluckers

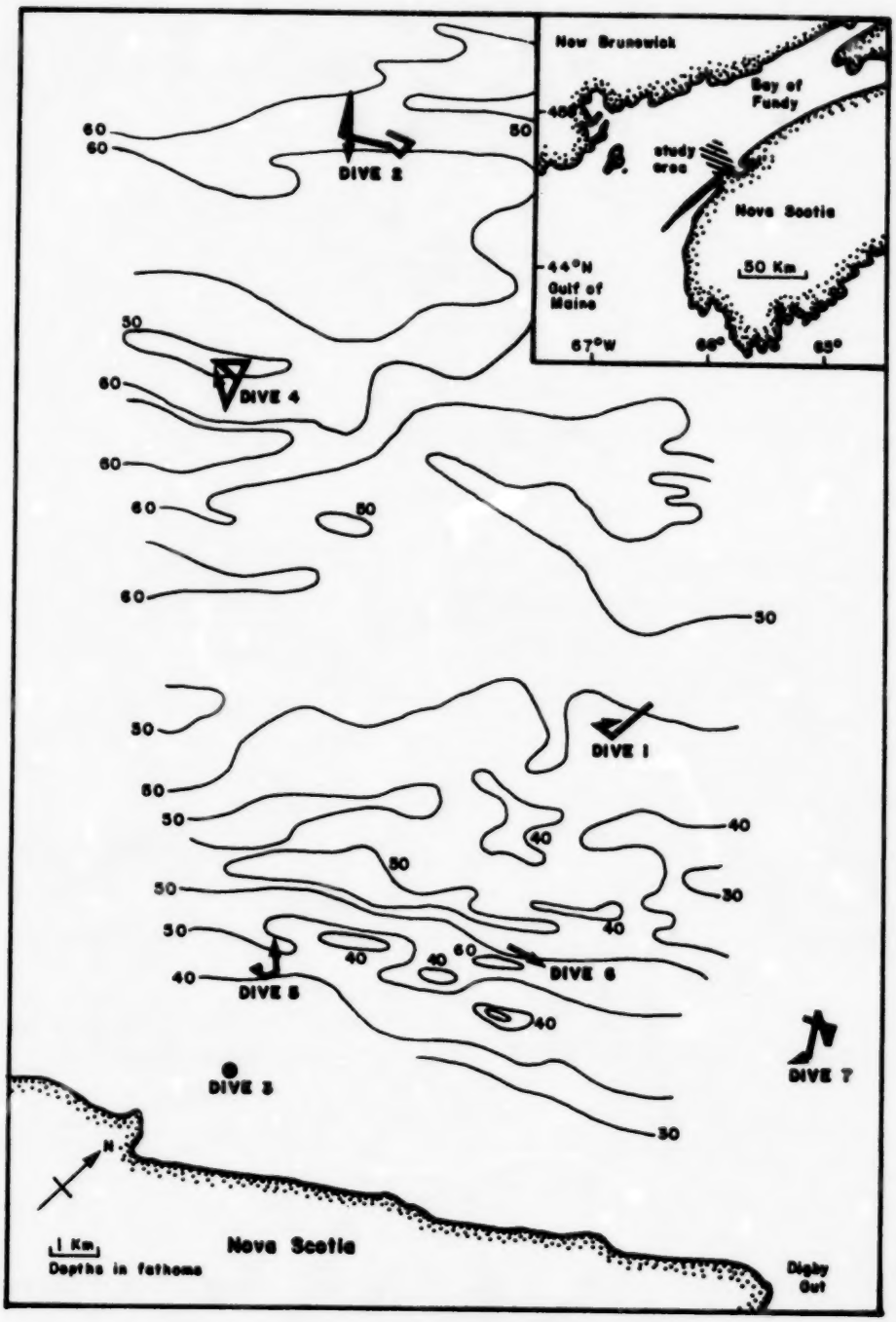


FIG. 1. Study area in the Lower Bay of Fundy.

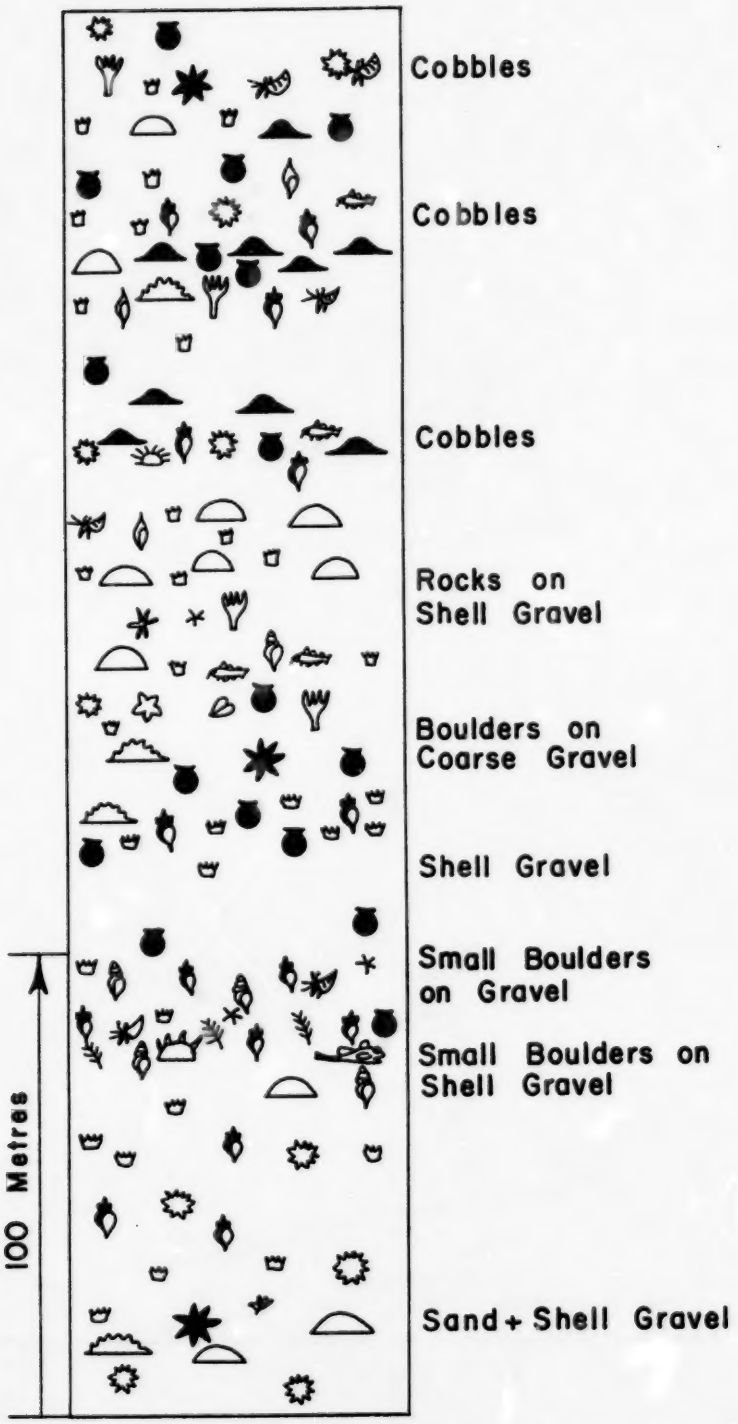


FIG. 2. Two-dimensional reconstruction of epifaunal observations from Dive 1.

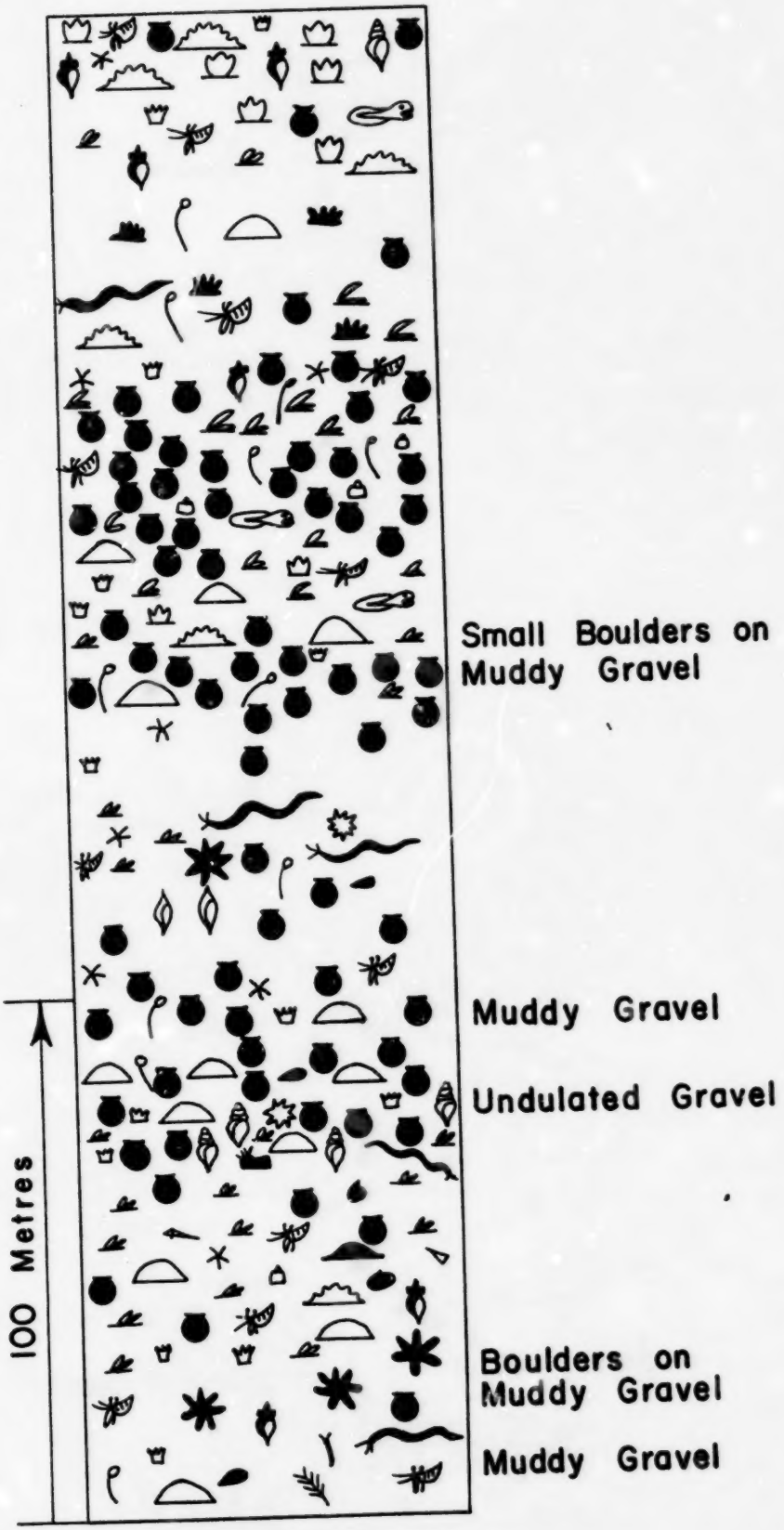


FIG. 3. Two-dimensional reconstruction of epifaunal observations from Dive 2.

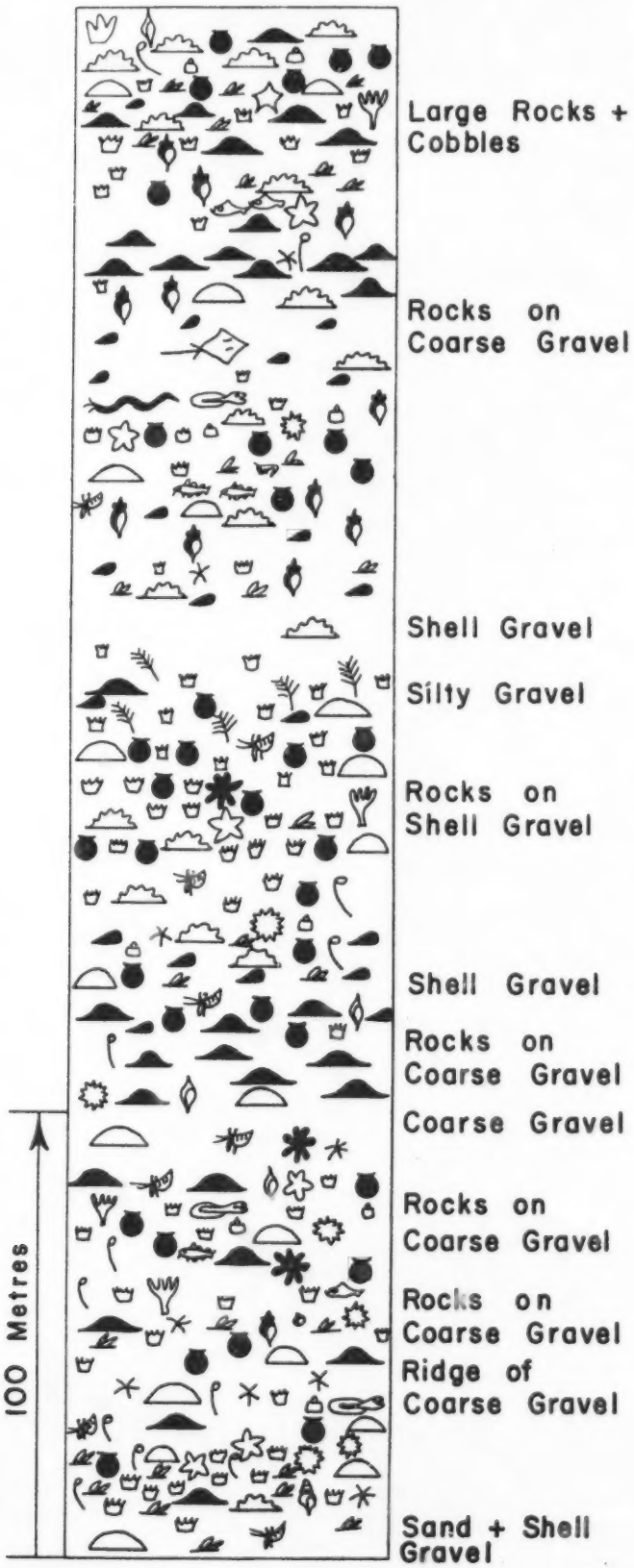


FIG. 4. Two-dimensional reconstruction of epifaunal observations from Dive 4.

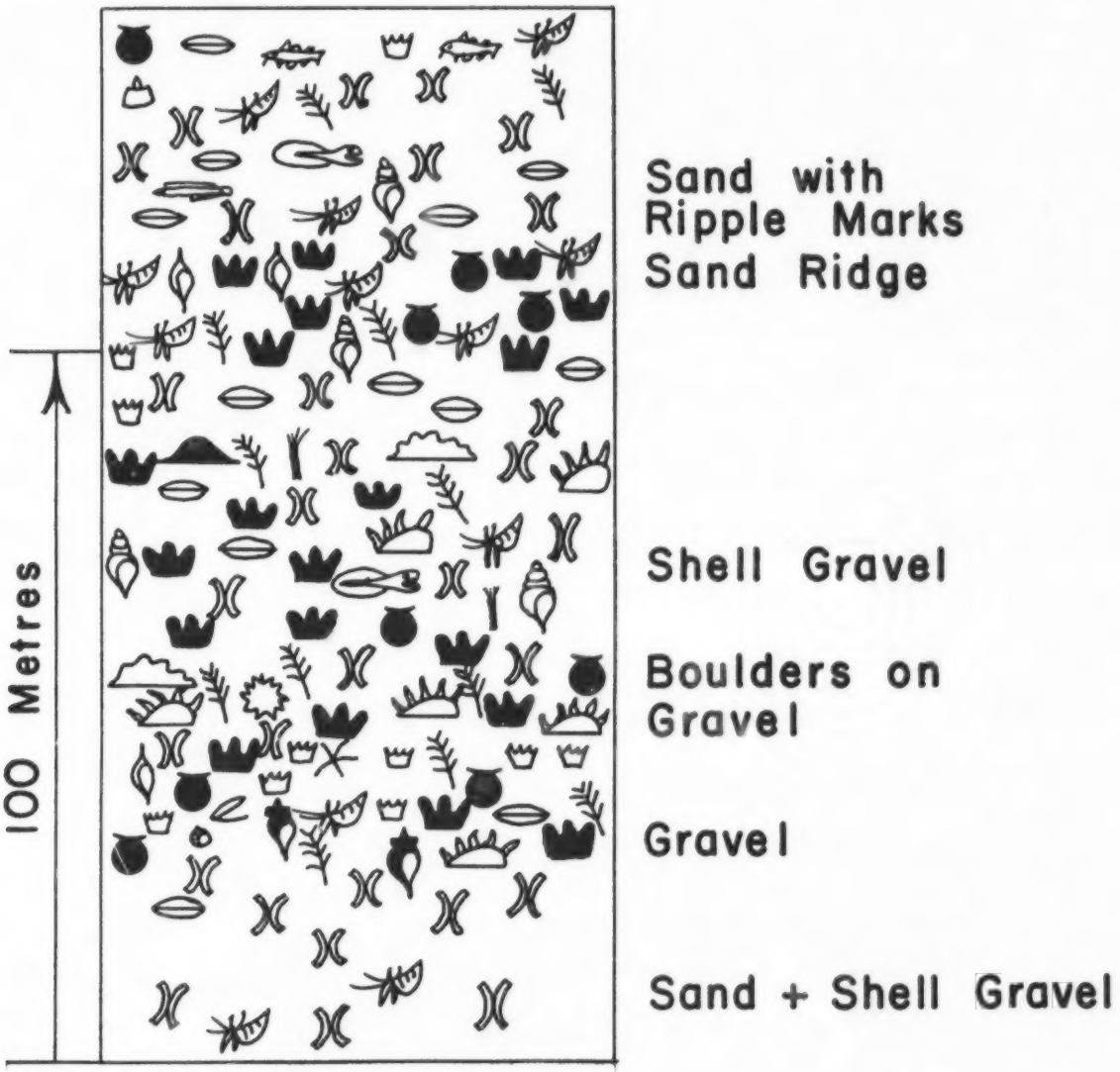


FIG. 5. Two-dimensional reconstruction of epifaunal observations from Dive 5.

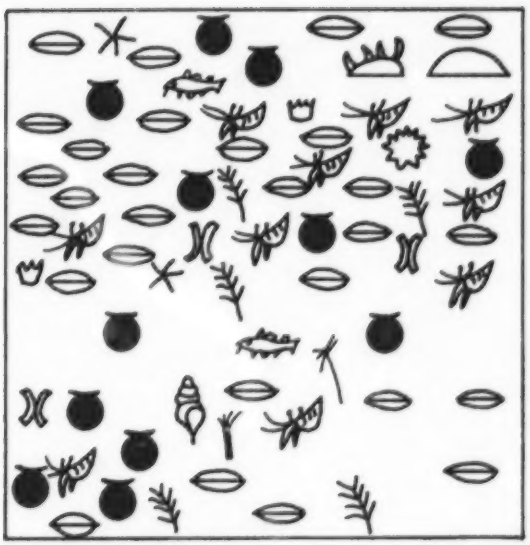


FIG. 6. Two-dimensional reconstruction of epifaunal observations from Dive 6.

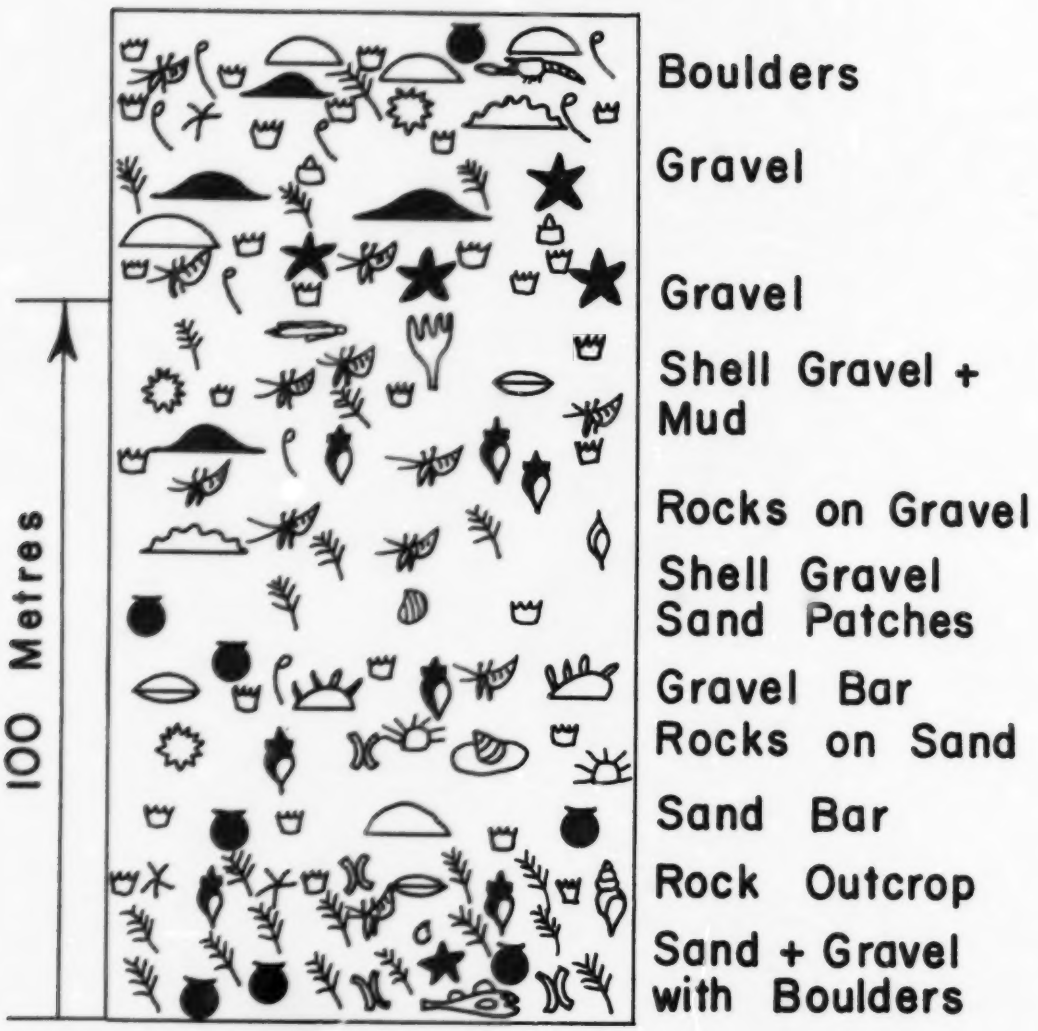


FIG. 7. Two-dimensional reconstruction of epifaunal observations from Dive 7.

FIG. 8. Percentage frequency of observations of fauna from all dives.